Ecological, Biosystematic, and Nomenclatural Notes on Scott's Spleenwort, × Asplenosorus ebenoides

KERRY S. WALTER, WARREN H. WAGNER, JR., and
FLORENCE S. WAGNER*

The best known and historically most interesting fern of the Appalachian region is the Scott's Spleenwort, ×*Asplenosorus ebenoides* (Scott) Wherry (Alston, 1940; Weatherby, 1949), a bigeneric hybrid between *Asplenium platyneuron* and *Camptosorus rhizophyllus*. The Ebony Spleenwort, *A. platyneuron* (L.) Oakes, has tall, pinnately compound leaves with shiny, blackish midribs; its veins are simple and bear parallel sori. The Walking Fern, *Camptosorus rhizophyllus* (L.) Link, has attenuate, simple leaves with green midribs; its veins are reticulate and bear arching sori. Proliferous leaves of the Walking Fern bear a plantlet at their long and thread-like tip. The hybrid fern combines the parental characteristics in a spectacular and often highly asymmetric manner.

The hybrid was first found near Philadelphia along the Schuylkill River around 1862 by a horticultural writer, Robert Robinson Scott, and has been known as Scott's Spleenwort ever since (Weatherby, 1949). Scott published a short description in Thomas Meehan's "Gardener's Monthly" in 1865 and called it *Asplenium ebenoides* (i.e., "like *ebeneum*," the then-current synonym of *platyneuron*). However, Meehan in an editorial note suggested that it might be a hybrid, and the following year the British naturalist Rev. M. J. Berkeley proposed its parents correctly (Weatherby, 1949).

A number of problems center around Scott's Spleenwort. There has been a question about the correctness of the epithet *ebenoides*. A fern considerd by some to be identical to it had been named *Asplenium hendersonii* by Houlston a decade and a half earlier than *A. ebenoides*.

It was assumed that Scott's Spleenwort was a sterile hybrid because in the original locality it occurred singly with the parents. However, around 1874, Julia L. Tutwiler, a teacher, discovered a large population of Scott's Spleenwort in Rock Hollow, near Havana in Hale Co., Alabama, a ravine later known to botanists as "Havana Glen." This apparently fertile population grew on a conglomerate rock of "pudding stone." Although Slosson (1902) proved hybridity experimentally using the gametophytes of the parents, fertility was demonstrated only much later by showing that the Havana Glen plants have doubled chromosomes and so are fertile and sexual (Wagner, 1954; Wagner & Whitmire, 1957).

Further studies have involved experimentally recreating fertile forms of ×*A. ebenoides* from sterile ones, backcrossing it, and demonstrating by chromatography that ×*A. ebenoides* contains the combined flavonoid compounds of both parents and that the 2*x* and 4*x* forms are alike in this respect (Wagner, 1954, 1956; Wagner & Whitmire, 1957; Wagner & Boydston, 1958; Smith & Levin, 1963).

*Division of Biological Sciences, University of Michigan, Ann Arbor, MI 48109.

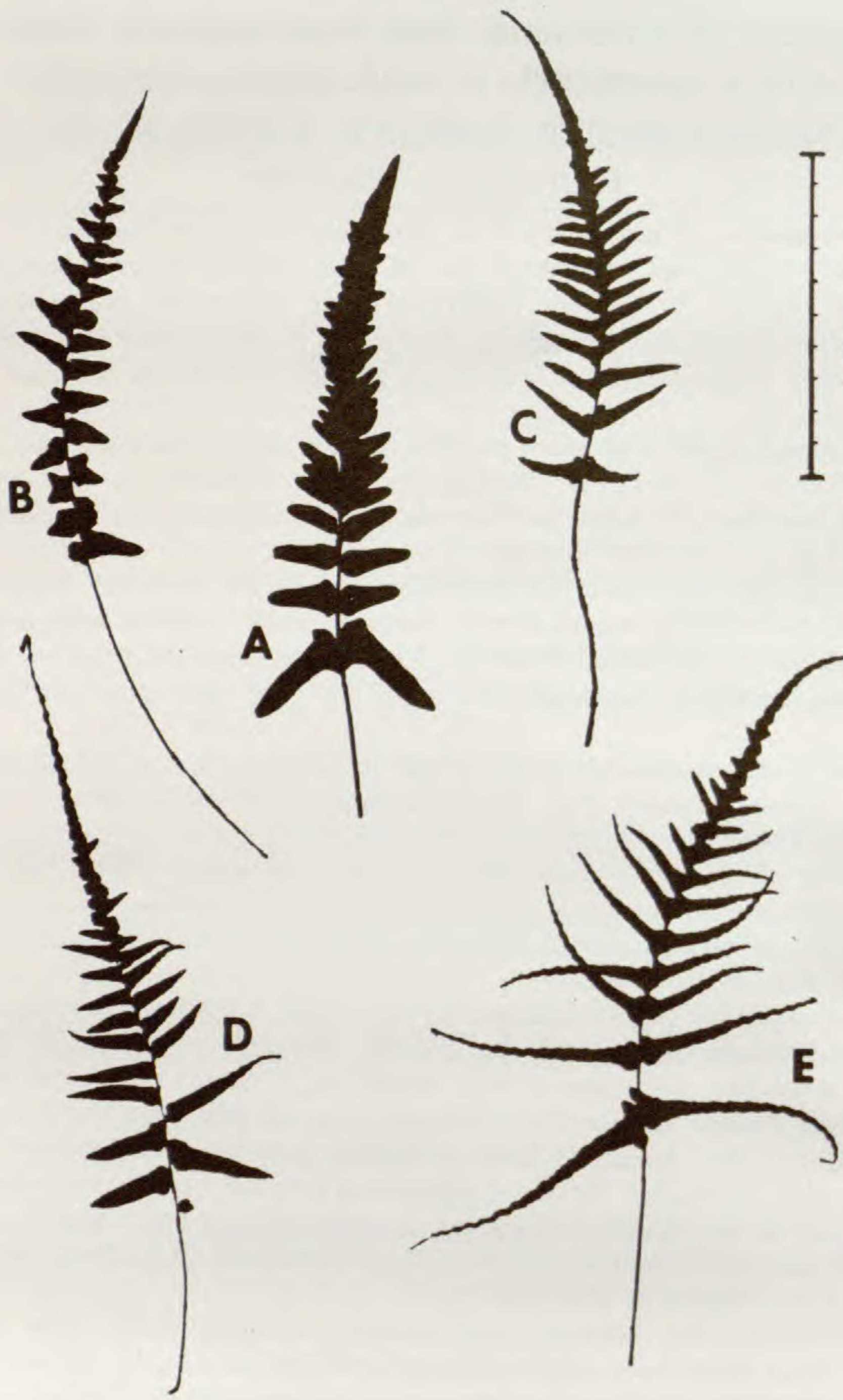

FIG. 1. Silhouettes. A. Type specimen (BM) of *Asplenium hendersonii* with stipe increased to approximate length of original description. B–E. ×*Asplenosorus ebenoides*. B. Sterile form, Mercer Co., KY, *Wagner 9127 & D. M. Smith* (MICH). C. Fertile form, Hale Co., AL, *Maxon & Pollard 335* (US). D, E. Sterile form, Giles Co., VA, *Wagner 10324.5* (MICH).

NOMENCLATURE

For over 75 years there has been some question about the proper epithet for ×*A. ebenoides*. Carl Christensen (1905) first suggested that it might be *Asplenium hendersonii* Houlston (1851), rather than *A. ebenoides* R. R. Scott (1866). The late C. V. Morton wrote (*in litt.*, 7 February 1968), "I have really no doubt that *hendersonii* is an earlier name for *ebenoides*. It is too bad to have this well-known name abandoned, but I see no alternative." To support this proposition, Morton sent a copy of his photograph of the type specimen of *A. hendersonii* from the British Museum.

We compared the type photo (silhouette is shown in *Fig. 1A*) with fronds of equivalent size of variations of unquestioned ×*A. ebenoides (Fig. 1B–E)*. We found two important differences: in *A. hendersonii*, the basal pinnae are much broader and rounded apically while in ×*A. ebenoides*, large fronds always have narrowly caudate tips, inherited from *Camptosorus rhizophyllus*. Careful examination frequently reveals a tiny plantlet or proliferation at the extreme apex *(Fig. 1D)*. *Asplenium hendersonii* has tips ca. 3–5 times broader than those of comparable ×*A. ebenoides* specimens.

The type specimen of *A. hendersonii* is annotated as folows: ". . . this plant was raised by Mr. Henderson ('Gardener to Earl Fitzwilliam at Wentworth') from spores, but from what country received he was unable to say." According to the original description (Houlston, 1851), the stipes are "about three inches long, and thinly covered with long brown narrow scales," the latter character not found in mature specimens of ×*A. ebenoides*.

Examination of the type of *A. hendersonii* revealed the existence of several significant differences. The sori of ×*A. ebenoides* are usually 1–3 mm long and only rarely are longer *(Fig. 2A)*; those of *A. hendersonii* are mostly 2–5 mm long *(Fig. 2B)*. Many sori and indusia in the upper half of the blades of *A. hendersonii* are double, and arise from two adjacent veins which meet one another, precisely as is found in the Hart's-Tongue, *Phyllitis*. The other distinctions of *A. hendersonii* can be readily explained if *Phyllitis*, rather than *Camptosorus*, is postulated as one of the parents. The "stubby" pinnae tips, the broad leaf apex, and the long sori are, of course, all features of *Phyllitis* and not *Camptosorus*.

We conclude, therefore, that *A. hendersonii* is really an ×*Asplenophyllitis* Alston, i.e., a spontaneous hybrid between *Phyllitis scolopendrium* and some species of *Asplenium*, perhaps the Sea Spleenwort, *A. marinum*, which is widespread along the coasts of England and Europe. Natural hybrids of *Phyllitis* with *Asplenium* are well known (Alston, 1940, listed three) as are artificial ones (Lovis, 1973). It is even possible that spores of *Phyllitis*, a very popular species in cultivation, germinated together with spores of an *Asplenium* in cultures sown by Henderson, giving rise to *A. hendersonii*. It is clear, therefore, that *hendersonii* is not the correct epithet for the Appalachian hybrid.

If Scott's Spleenwort is kept in the genus *Asplenium*, the name should appear as *Asplenium* ×*ebenoides*, using the multiplication sign, as prescribed by the International Code of Botanical Nomenclature, to indicate its hybrid nature. As to the rare fertile form, it has been argued elsewhere (Wagner, 1969) that it is irrelevant whether


A
B
C
1 cm

the plant is sterile or fertile. Since it is a hybrid, diploid or tetraploid, the hybrid sign should be used, and the cytological condition be indicated by a descriptive phrase "sterile diploid form" or "fertile tetraploid form." In the case at hand, the fertile tetraploid form has been produced in culture directly from the sterile form (Wagner & Whitmire, 1957).

However, we believe the name of the plant should be ×*Asplenosorus ebenoides* (Scott) Wherry, with the multiplication sign before the generic name, as this plant is, according to most present thinking, an intergeneric hybrid (Mickel, 1974). *Camptosorus* should be maintained as a genus because its differences from *Asplenium* are of the same magnitude as those of other genera in the Asplenioideae such as *Diellia* and *Phyllitis*. There is no reason to abandon the genus *Camptosorus* simply because it hybridizes with *Asplenium*. Lovis (1973) discussed intergeneric fern hybrids and pointed out that not only are there *Asplenium* × *Camptosorus* (= ×*Asplenosorus* Wherry) hybrids known, but *Asplenium* × *Phyllitis* (= ×*Asplenophyllitis* Alston), *Asplenium* × *Ceterach* (= ×*Asplenoceterach* D. E. Meyer), *Camptosorus* × *Phyllitis*, and *Asplenium* × *Pleurosorus* as well.

STATUS OF THE HAVANA GLEN POPULATION

This report is based upon field studies by W. H. Wagner and K. S. Walter in 1971 and by Dr. R. R. Haynes of the University of Alabama in 1978; the most recent previous report is that by Wherry and Trudell (1930). The locality is approximately 40 km south of Tuscaloosa outside of Havana. Winters are relatively mild, with the leaves off the deciduous trees and shrubs, and most annual herbaceous shoots withered.

What we call "Havana Glen" is known locally as "Rock Hollow." It is owned by Mrs. R. B. Lavender, of Mobile, Alabama, who has strict rules governing who can enter the area and whether logging is permitted in or near it. We discussed the past history of the unusual fern populations with her relative, Mrs. T. N. Lavender, who remembered the botanists who had visited, especially H. E. Ransier of Manlius, New York, who traveled to Havana at least twice[1].

Miss Tutwiler originally described the habitat as "about eight miles from the Black Warrior River . . . The soil is either red clay or a mixture of sand and gravel except in the creek and river bottoms. The country is rolling, covered with hills

[1]According to our records, the following botanists visited the locality. Most made collections now deposited in well-known herbaria: 1884—Julia T. Tutwiler; 1890—J. W. A. Wright; 1892—L. T. Ward; 1896—L. Underwood; 1900—C. L. Pollard and W. R. Maxon; 1905—E. A. Smith; 1907—J. W. Moreland; 1912—G. L. Fischer; 1918, 1920—E. W. Graves; 1928, 1933—H. E. Ransier; 1929—E. T. Wherry and H. W. Trudell; 1967, 1974—B. E. Dean; 1971—W. H. Wagner, Jr. & K. S. Walter; 1978—R. R. Haynes.

FIG. 2. Comparison of ×*Asplenosorus ebenoides* and Asplenium hendersonii. A–B. ×*Asplenosorus ebenoides*. A. Abaxial side of frond near tip showing short, unpaired sori, *Wagner 76016* (MICH). B. Same, *Wagner s. n.*, 5 Dec 1955 (MICH). C. Type specimen of *Asplenium hendersonii*. Abaxial side of frond from a comparable area showing longer, paired sori, and broader lamina. FIG. 3. Havana Glen, Hale Co., AL, habitat for ×*Asplenosorus ebenoides*, showing moss- and lichen-covered boulders of conglomerate rock.

about 200 feet above sea level" (Dean, 1969). The Hollow lies along a brook below farm fields 1.2 km NNW of the Havana Post Office. The valley side where the rock crops out slopes approximately 20–35° *(Fig. 3)*. The slopes are occupied mainly by deciduous trees; toward the bottom of the valley increasing numbers of mountain laurel, *Kalmia latifolia*, appear. Haynes (pers. comm.) considers the forest an excellent representative of the deciduous forest of Alabama, "as natural as you can get in the state." It shows no evidence of logging. Some of the prominent trees include *Quercus alba*, *Q. rubra*, *Q. prinus*, *Fagus grandifolia*, *Illicium floridanum*, *Liriodendron tulipifera*, and *Magnolia macrophylla*. Scattered shrubs and woody vines include *Vitis* spp., *Smilax* spp., *Euonymus americanus*, and *Hydrangea quercifolia*. The forest is somewhat open and park-like.

The rock outcrops in the valley are 0.5–8 m tall, and most are north-facing. Wherry and Trudell (1930) described the rock as a brownish conglomerate of siliceous pebbles in a ferruginous and slightly calcareous cement and the soil reaction at the roots of the ×*Asplenosorus* plants as being minimacid[2]. The more or less crowded pebbles in the sandy substratum are smoothly rounded, indicating stream wear prior to consolidation.

The rocks are coated with green bryophytes and/or fine, white, crustose lichens. Those collected in association with ×*Asplenosorus ebenoides* were identified by Howard A. Crum of the University of Michigan Herbarium. The crustose lichen is a species of *Parmelia*. The most abundant mosses are *Anomodon attenuatus* (Hedw.) Hub. *(Wagner 71167)* and *Bryoandersonia illicebrum* (Hedw.) Robins. *(71168)*. Together with the liverwort *Metzgeria furcata* (L.) Dum. *(71169)* were mixed small quantities of the moss *Brachythecium oxycladon* (Brid.) Jaeg. & Sauerb. and two liverworts of the genera *Radula* and *Frullania*. Two additional mosses occur frequently, viz. *Fissidens cristatus* Wils. ex Mitt. *(71170)* and *Anomodon rostratus* (Hedw.) Schimp. *(71171)*. Vouchers are deposited in the University of Michigan Herbarium (MICH).

The majority of ferns and herbs occur on and around the rock outcrops rather than on the leaf-covered forest floor. Scattered plants of *Polystichum acrostichoides*, *Dryopteris marginalis*, and *Hexastylis* sp. may grow in the flatter, non-rocky areas, but all three tend to be more common at and around the rock bases. On the boulders themselves are such herbs as *Mitchella repens* and *Saxifraga virginiana*. The latter, together with *Hepatica americana*, may sometimes be found in bloom as early as January or February.

In addition to the *Polystichum* and *Dryopteris*, we found nine additional fern species or hybrids at the locality. The most common are *Polypodium polypodioides*, *Asplenium platyneuron*, and *A. trichomanes*. Along the upper slopes are large plants of *Cheilanthes lanosa*. Masses of tangled green filaments in sheltered, deeply shaded crevices of the rock are clonal gametophytes of the filmy fern genus *Trichomanes*. A large patch of sporophytes of *T. boschianum* occurs on the vertical wall in a recess of one of the larger cliffs.

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[2]Donald Farrar reports (pers. comm.) that this substrate is Pottsville sandstone of Pennsylvanian age, with a slightly acidic pH (5 to 6).

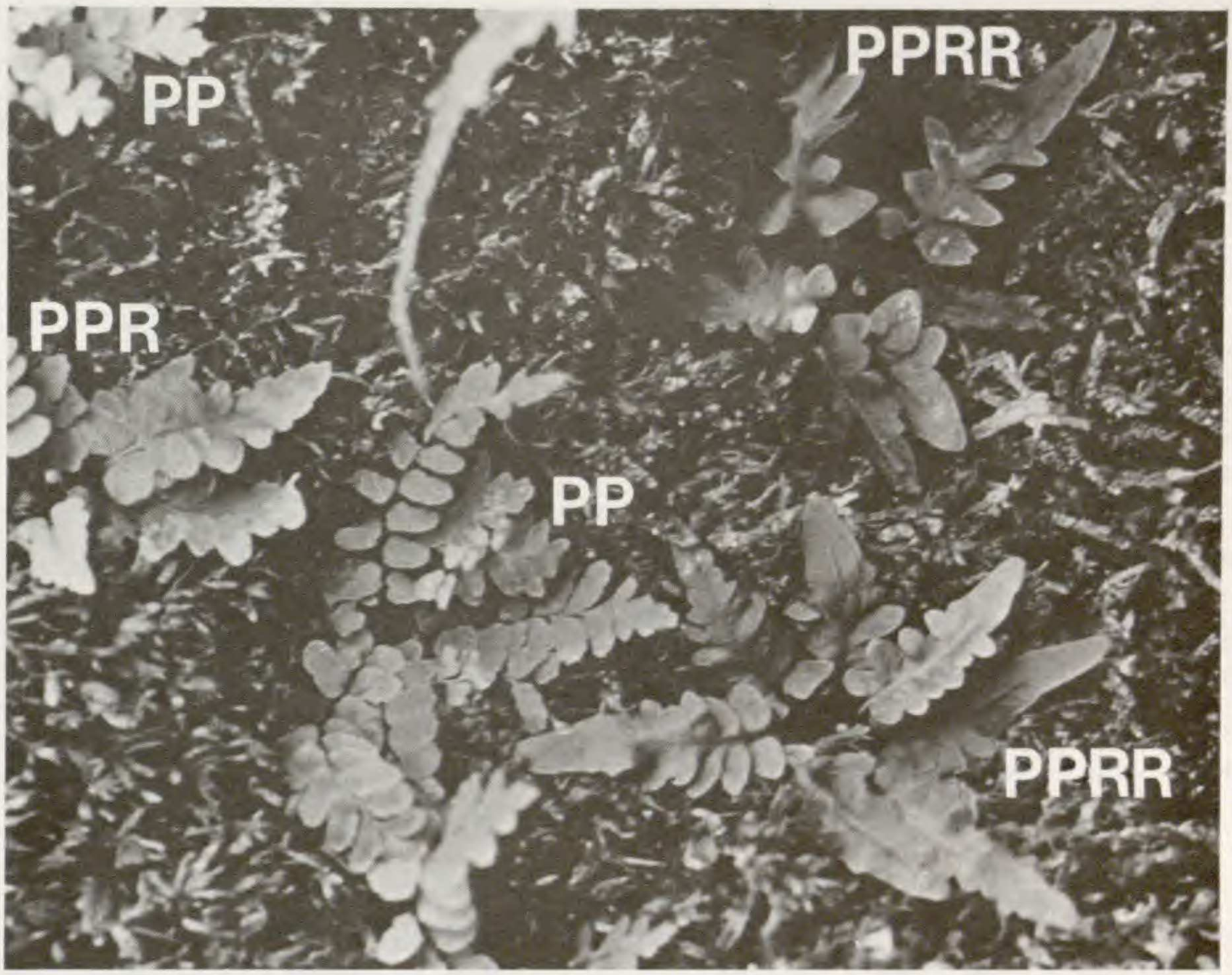

FIG. 4. Young spleenworts on moss-covered rock at Havana Glen, AL. PPR = ×*Asplenosorus boydstonae* (= *Asplenium platyneuron* ×*Asplenosorus ebenoides*). PP = *A. platyneuron*. PPRR = × *A. ebenoides*.

We did not find *Camptosorus rhizophyllus* in our explorations. Wherry and Trudell (1930) had the same experience, although Wherry wrote (*in litt.*, 1972) that "The St. John brothers told us that they had visited the 'glen' and found . . . the two parents," and the original discoverer, Miss Tutwiler, had written that she found walking fern there (Dean, 1969). It is possible that all of these people were in some other valley nearby. For example, Wherry, (op. cit.) wrote,

> After I visited the "Glen" I thought it would be interesting to see what was in other ravines nearby. . . . Assuming that I started north, the road descended down the conglomerate-rock escarpment (on the east side of the Glen) and joined an east-west road running along the valley. I walked eastward along this road, repeatedly ascending small cliffs, and entering small ravines, probably for a distance of a mile. *Asplenium platyneuron* was conspicuous everywhere; but the *ebenoides* did occur repeatedly on both moist and dry rock surfaces.

Although Wherry did not find *Camptosorus*, his finding other nearby ravines suggests that a detailed exploration of the whole area in the vicinity of Havana Glen might be profitable. Not only might populations of *Camptosorus* turn up, but other interesting pteridophytes as well.

FIG 5. Silhouettes of medium- and large-sized fronds of plants collected at Havana Glen, AL, and cultured in greenhouse. Left = ×*Asplenosorus boydstonae*. Right = *Asplenium platyneuron*.

THE TETRAPLOID EBENOIDES POPULATION AND ITS BACKCROSSES

In view of Wherry's comments quoted above, it is possible that *A.* ×*ebenoides* is considerably more widespread in the Havana area than has been believed. The following is based upon our observations made during the 1970's. The fertile Scott's spleenwort is much less common in the Glen than either *A. platyneuron* or *A. trichomanes*. Juvenile specimens are abundant intergrown with juveniles of other

spleenworts. The number of ×*A. ebenoides* plants is estimated to be between 200 and 300. Most are small, the number of fronds ranging from 3 to 7 and the frond size 3 cm or less *(Fig. 4)*. Isolated, single plants are exceptional; most of the individuals are in groups of several to 2–3 dozen. Plants with sori had fronds as short as 4 cm long including the petiole when they occurred in relatively dry, exposed places, and up to more than 14 cm long in damper, shady places. We observed fewer than three dozen soriferous plants, these widely scattered and not confined to a single area.

No plants, even the largest, showed frond-tip proliferations visible to the naked eye, although such proliferations have been reported in the past. According to Wherry (pers. comm.), the proliferous tip illustrated by him and Trudell (1930) was not from the Glen, but from outcrops of dry conglomerate half a mile or so east. Functional proliferations must be extremely rare, and vegetative reproduction is of little or no importance in maintaining the population. Virtually all of the plants evidently arise from spores.

The small plants grow slowly, especially during dry years (even though in culture they may be vigorous and fast growing, almost becoming greenhouse weeds). Similarly, many of the spleenwort populations in peninsular Florida are noted for waxing and waning year to year, depending upon climate. During drought, populations become reduced to tiny plants, many so small as to simulate sporelings. In moister periods, the spleenworts spring up and form large, soriferous plants of mature form. The conditions at Havana Glen may be similar.

In the Appalachian spleenworts, backcross hybrids are rare, the exception being the sterile triploid hybrid ×*Asplenosorus pinnatifidum* × *Asplenium montanum*, (= ×*Asplenosorus trudellii* (Wherry) Mickel) (W. Wagner, 1954). This is so common in some localities that it must have some method of propagation, although the spores are highly abortive, and meiosis involves both univalents and bivalents.

Some backcrosses of ×*Asplenosorus ebenoides* have been produced in the laboratory, including the tetraploid, fertile form with its parents. The backcross to *Asplenium platyneuron* (= ×*Asplenosorus boydstonae* K. S. Walter) was first synthesized experimentally at the University of Michigan (Wagner, 1956); and this as well as the backcross to *Camptosorus rhizophyllus* at Fernwood, Niles, Michigan (Wagner & Boydston, 1958).

Backcross leaves are intermediate in structure. The *A. platyneuron* backcross has leaves like *A. platyneuron* but possesses a caudate tip shorter than that of ×*A. ebenoides*. The leaves of the *Camptosorus rhizophyllus* backcross look like irregularly lobed Walking Fern leaves. In describing the *A. platyneuron* backcross, we noted that it "has very little likelihood of ever being discovered in the wild, except possibly in one small area in Hale Co., Alabama," by which we meant Havana Glen. A particularly fine mixed colony was found by K. S. Walter in 1971 on the east-facing side of a boulder. Here we encountered the first wild examples of ×*Asplenosorus boydstonae*. This boulder was approximately 1 m high and 2.5 m wide. Mosses covered roughly one-half of its surface; the remainder was white with crustose lichens. In the mosses were 35 plants of ×*Asplenosorus ebenoides*, 12 large, fertile, up to 15 cm long, and the remainder small, like those in *Fig. 4*. There were 23

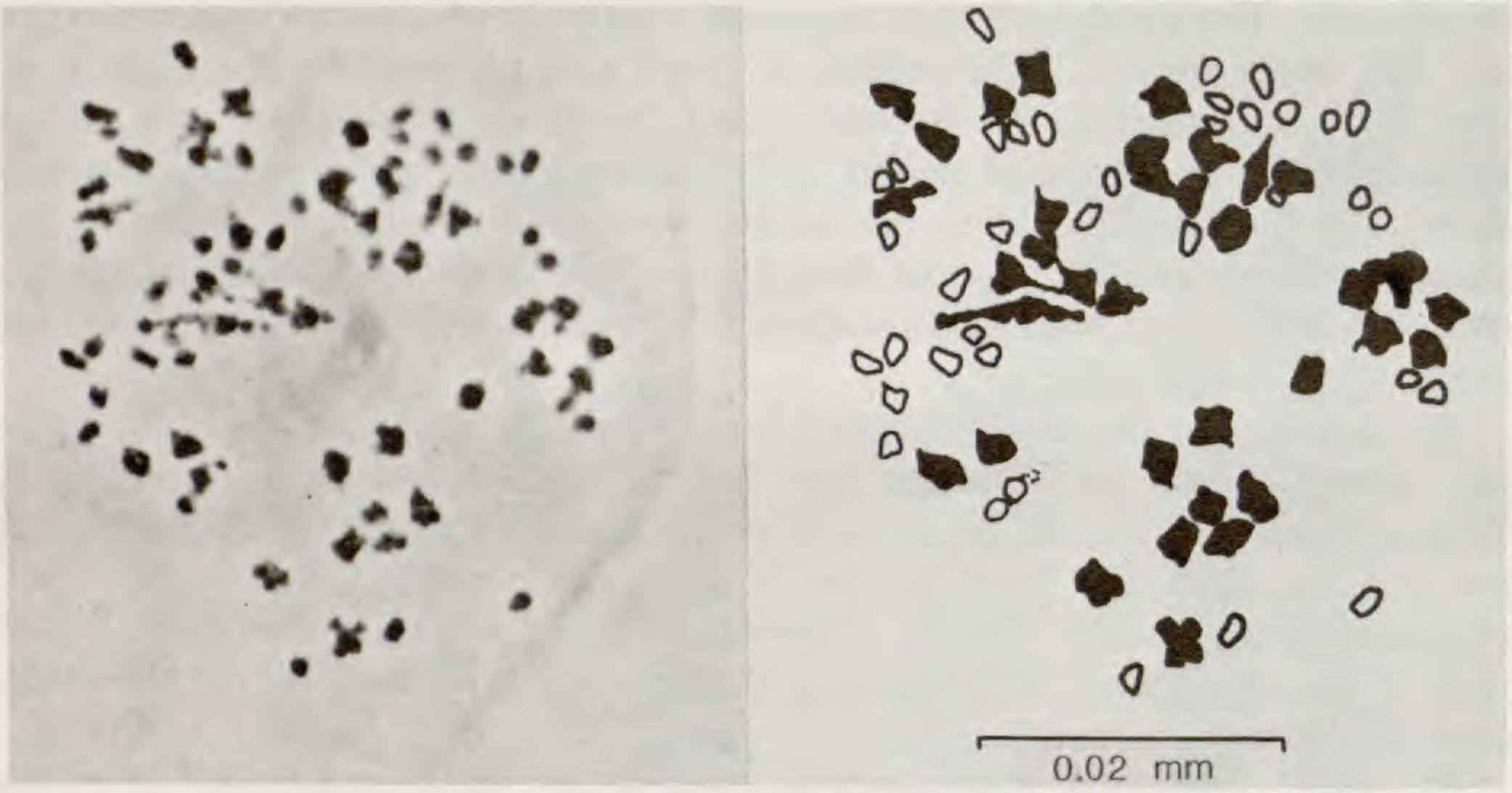

FIG 6. Chromosomes of a natural ×*Asplenosorus boydstonae* hybrid from Havana Glen, AL, showing 36 pairs (PP) and 36 singles (R).

plants of *Asplenium platyneuron*, of which only four were fertile and up to 15 cm long. One small plant of *A. trichomanes* was present.

Growing with them were three plants of small size but obviously greater blade division than in equal-sized plants of typical ×*Asplenosorus ebenoides* (see *Fig. 4*). Two specimens were taken alive for culture purposes. We grew them to full size *(Fig. 5)*, and found them to be morphologically identical with the experimentally produced backcrosses. They have 108 chromosomes (i.e., the triploid condition, with 36 pairs of chromosomes from ×*Asplenosorus ebenoides* and 36 singles from *Asplenium platyneuron, Fig. 6*), as had the laboratory specimens (Wagner & Boydston, 1956, pl. V, figs. A_1–A_4).

The discovery of the sterile backcrosses, ×*Asplenosorus boydstonae*, at Havana Glen may be the first case in pteridology in which a taxon was produced initially in the laboratory under experimental conditions and only discovered later as a wild plant growing under natural conditions.

We wish to express thanks to R. R. Haynes, Clive Jermy, Mrs. T. N. Lavender, Mary R. Rainey, Donald Rainey, James Rainey, the late Edgar T. Wherry and to the late Blanche E. Dean for their assistance in this study.

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